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Human muscle power generating capability during cycling at different pedalling rates

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The effect of different pedalling rates (40, 60, 80, 100 and 120 rev min⁻¹) on power generating capability, oxygen uptake (\dot{V}_{O_2}) and blood lactate concentration $[La]_b$ during incremental tests was studied in seven subjects. No significant differences in $\dot{V}_{O_{2,max}}$ were found (mean \pm s.d., 5.31 ± 0.13 l min⁻¹). The final external power output delivered to the ergometer during incremental tests ($P_{I,max}$) was not significantly different when cycling at 60, 80 or 100 rev min⁻¹ (366 ± 5 W). A significant decrease in $P_{I,max}$ of ~ 60 W was observed at 40 and 120 rev min⁻¹ compared with 60 and 100 rev min⁻¹, respectively ($P < 0.01$). At 120 rev min⁻¹ there was also a pronounced upward shift of the \dot{V}_{O_2} -power output (\dot{V}_{O_2} - P) relationship. At 50 W $\Delta\dot{V}_{O_2}$ between 80 and 100 rev min⁻¹ amounted to $+0.43$ l min⁻¹ but to $+0.87$ l min⁻¹ between 100 and 120 rev min⁻¹. The power output corresponding to 2 and 4 mmol l⁻¹ blood lactate concentration ($P_{[La]2}$ and $P_{[La]4}$) was also significantly lower (> 50 W) at 120 rev min⁻¹ ($P < 0.01$) while pedalling at 40, 60, 80 and 100 rev min⁻¹ showed no significant difference. The maximal peak power output ($P_{M,max}$) during 10 s sprints increased with pedalling rate up to 100 rev min⁻¹. Our study indicates that with increasing pedalling rate the reserves in power generating capability increase, as illustrated by the $P_{I,max}/P_{M,max}$ ratio (54.8, 44.8, 38.1, 34.6, 29.2%), the $P_{[La]4}/P_{M,max}$ ratio (50.4, 38.9, 31.0, 27.7, 22.9%) and the $P_{[La]2}/P_{M,max}$ ratio (42.8, 33.5, 25.6, 23.1, 15.6%) increases. Taking into consideration the $\dot{V}_{O_{2,max}}$, the $P_{I,max}$ and the reserve in power generating capability we concluded that choosing a high pedalling rate when performing high intensity cycling exercise may be beneficial since it provides greater reserve in power generating capability and this may be advantageous to the muscle in terms of resisting fatigue. However, beyond 100 rev min⁻¹ there is a decrease in external power that can be delivered for a given \dot{V}_{O_2} with an associated earlier onset of metabolic acidosis and clearly this will be disadvantageous for sustained high intensity exercise. *Experimental Physiology* (2000) 85.1, 117–124.

Human locomotory performance is dependent upon the ability of skeletal muscle to generate mechanical power, and sustain that power – that is, resist fatigue. Not surprisingly the factors influencing this capability have attracted the attention of many investigators dating back to and beyond the beginning of this century (see e.g. Benedict & Cathcart, 1913; Krogh & Lindhard, 1920; Hill, 1922; Lupton, 1923; Dickenson, 1928; Wilkie, 1960, 1981; Carnevale & Gaesser, 1991; McNaughton & Thomas, 1996).

However, although there are a number of studies which have examined the maximum power of human locomotory muscles, and many more which have examined the constraints and limitations to sustained exercise – especially with respect to aerobic and anaerobic energy supply – rather few data are available from studies which have examined, in the same

subjects, the relationship between maximum power and the power delivered in sustained exercise, and there are almost no data on the effect that movement frequency has on that relationship.

In part, this paucity of data is due to the technical difficulty of measuring maximal power output at a constant known movement frequency in human locomotion. In seeking to address this difficulty, one of us developed an isokinetic cycle ergometer which enabled the maximum power generated by the main locomotory muscles to be measured over a range of movement frequencies (Sargeant *et al.* 1981). Subsequently, the ergometer system was modified so that the power could be measured continuously at the foot–pedal interface either during submaximal exercise, or during a maximum effort with the system switched to its isokinetic

Table 1. Characteristics of the subjects

Subject	Age (years)	Height (cm)	Body mass (kg)	$\dot{V}_{O_{2,max}}$ (l min ⁻¹)
W.K.	28	178	74	5.683
A.R.	32	191	80	5.836
A.K.-I.	24	200	82	5.417
T.N.	23	190	72	4.687
P.K.	24	191	92	4.844
J.W.	21	176	79	6.416
T.D.	26	186	75	5.571
Mean \pm S.D.	25.4 \pm 3.6	187.7 \pm 8.3	79.1 \pm 6.7	5.493 \pm 0.590

mode (Beelen & Sargeant, 1991; Beelen *et al.* 1994). It is the latter modified system which we have used in the present study of the relationship between maximum available leg extensor power at different movement frequencies and the power delivered during submaximal exercise. As objective indicators of sustainable power output we have used the external power delivered in exercise eliciting: (i) maximal oxygen uptake ($\dot{V}_{O_{2,max}}$), (ii) blood lactate concentration of 4 mmol l⁻¹ ($P_{[La]4}$), and (iii) blood lactate concentration of 2 mmol l⁻¹ ($P_{[La]2}$), as proposed by previous authors as predictors of exercise tolerance (Sjödén & Jacobs 1981; Kinderman *et al.* 1979; Tanaka & Matsuura, 1984; Henritze *et al.* 1985; Zoladz *et al.* 1993, 1998).

From previous studies (Sargeant *et al.* 1981; McCartney *et al.* 1983; Sargeant, 1987; Beelen & Sargeant, 1991) it is known that in cycling exercise maximum power demonstrates a parabolic relationship with movement frequency (pedalling rate), such that the optimum velocity for maximum power (V_{opt}) occurs around 120 rev min⁻¹. By definition this means that a given constant submaximal power output would require proportionally less of the maximum available power to be used at 120 rev min⁻¹ pedalling rate compared to slower (or faster) rates. The obverse of this is that the reserve of power generating capability in the active musculature will be greater at 120 rev min⁻¹. All other things being equal, it would seem strategically advantageous to choose the pedalling rate at which the greatest reserve is available since this would presumably allow exercise to be sustained for longer (but see Sargeant & Jones, 1995; Sargeant, 1996, for discussion of this point). Clearly, this would not be true, however, if there was a disproportionate increase in the energy cost for power delivered at 120 rev min⁻¹ associated with increased reliance on anaerobic energy supply and associated changes in acid-base status.

In the present study we have sought to test the hypothesis that, within the normal locomotory range of movement frequency, it is: (i) advantageous to choose faster rather than slower pedalling rates in order to maintain the greatest reserve of muscle power and thus resist fatigue and prolong exercise; (ii) that this apparent advantage will be negated at

the fastest rates attainable by an increase in the energy cost for the power delivered, and increased anaerobiosis, necessitating a compromise in terms of the optimum rate for sustaining power output and resisting fatigue.

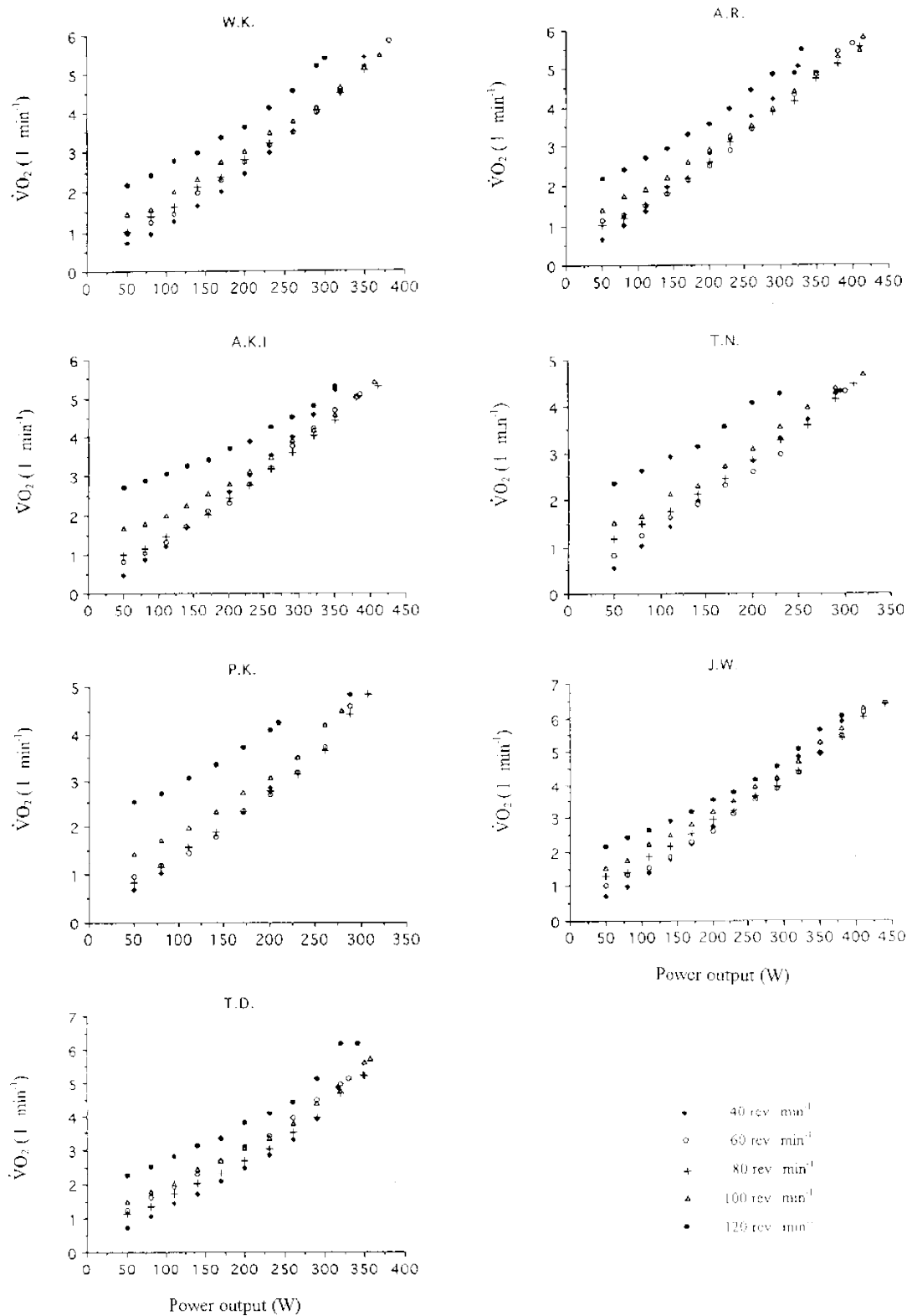
METHODS

Seven healthy physically active males volunteered to participate in this study. All of them had already had experience in laboratory tests and were familiarised with cycling at the pedalling frequencies used in this study. The physical characteristics of the subjects are given in Table 1.

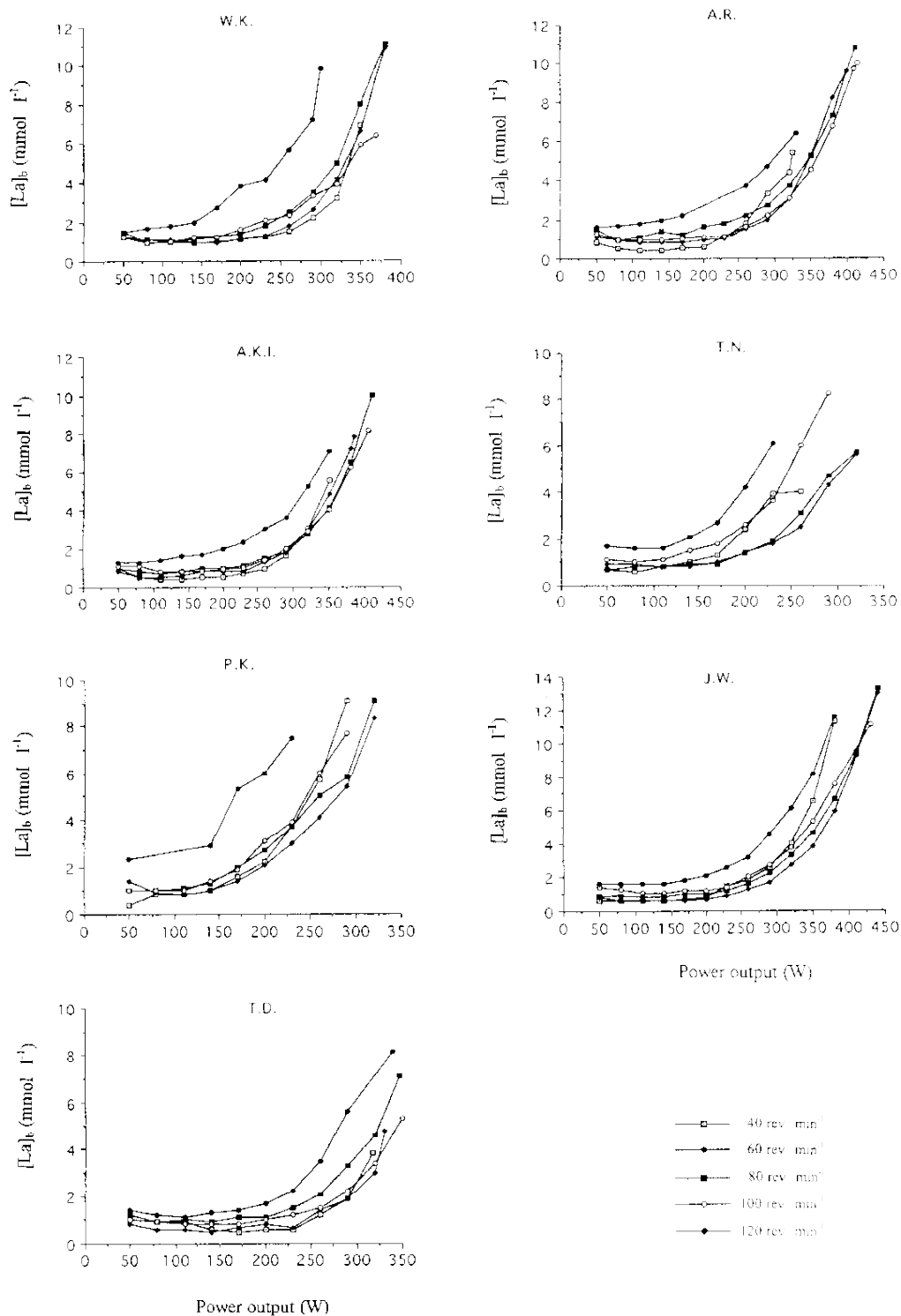
The purpose of the first series of experiments was to determine the maximal peak power output ($P_{M,max}$) at different pedalling rates at constant velocity on an isokinetic cycle ergometer (Beelen *et al.* 1994). Subjects performed 10 s maximal sprints at six different pedalling rates of 40, 60, 80, 100, 120 and 140 rev min⁻¹. Sprints were separated by a recovery period of at least 15 min. During each sprint, the forces exerted on the pedals were continuously monitored by strain gauges mounted in the pedals, with a frequency of 150 samples per revolution. A static calibration of the force pedals was performed using a lever-arm constriction as described in detail by Beelen *et al.* (1994). Forces up to 1500 N were generated on the pedals via the lever arm, and the responses were found to be linear over the entire range.

During experiments the forces vertical and horizontal to the pedal surface were measured to allow calculation of tangential force (that is, effective force), and power was calculated from this force and crank velocity. For each 10 s maximal sprint $P_{M,max}$ was determined as the mean of three consecutive values in which the highest observed power for one complete revolution occurred. Values for $P_{M,max}$ were averaged for the right and left leg (for details see Beelen *et al.* 1994).

During a second series of experiments, oxygen uptake (\dot{V}_{O_2}), blood lactate concentration $[La]_b$ and forces exerted on the pedals during incremental tests at the same pedalling frequencies were measured with the exception of 140 rev min⁻¹. Tests were performed in random order. Before each experiment care was taken to provide the same cycling position by adjusting the level of the saddle and handlebars. All tests were designed in such a way that after a 6 min resting period, during which rest values were collected, the subjects began to cycle at a power output of 50 W for a period of 3 min. The power output (P) over the whole test was increased by 30 W every 3 min (Zoladz *et al.* 1995). The subjects were verbally encouraged to continue cycling until exhaustion. The test was stopped when the subjects could no longer maintain the required pedalling frequency.

**Figure 1**

Individual data of oxygen uptake ($\dot{V}O_2$) reached during incremental tests performed at pedalling rates of 40, 60, 80, 100 and 120 rev min^{-1} .

**Figure 2**

Individual data of blood lactate concentration ($[La]_b$) reached during incremental tests performed at pedalling rates of 40, 60, 80, 100 and 120 rev min^{-1} .

Forces generated on the pedals were recorded during the third minute of each incremental step.

Throughout the test \dot{V}_{O_2} was measured breath by breath (Oxycon gamma, Mijnhardt, The Netherlands). Blood lactate concentration was determined in samples of arterialised blood taken from the finger tip at the end of each 3 min step and analysed enzymatically, using a Lactate Analyser (YSI, Yellow Springs, USA).

The final power output stage during the incremental tests was defined as the highest mechanical power output attained ($P_{I,max}$) in this test. In those cases when the test was stopped before the end of an incremental stage, $P_{I,max}$ was calculated from the previous completed stage plus a time weighed proportion of the uncompleted stage. Power output corresponding to 2 and 4 mmol l⁻¹ blood lactate concentration ($P_{[La]2}$ and $P_{[La]4}$) was determined by plotting individual data of blood lactate concentration against power output (see Sjodin & Jacobs, 1981).

All experiments were performed under constant room temperature (18 °C) and humidity (55%).

Data represent means \pm s.d. Statistical significance was tested by analysis of variance for repeated measures.

RESULTS

$\dot{V}_{O_{2,max}}$ and \dot{V}_{O_2} - P relationship

The results of our study showed no significant difference in $\dot{V}_{O_{2,max}}$ when cycling at pedalling rates in the range 40–120 rev min⁻¹. The mean (\pm s.d.) value of $\dot{V}_{O_{2,max}}$ was 5.31 ± 0.13 l min⁻¹. In Fig. 1 the \dot{V}_{O_2} - P data for the incremental tests are shown for all pedalling rates and for each subject. In each subject and at all pedalling rates there was a progressive increase in \dot{V}_{O_2} as the power output delivered increased. At low power outputs \dot{V}_{O_2} was lowest at the slowest pedalling rate, 40 rev min⁻¹, and highest at the fastest pedalling rate studied, 120 rev min⁻¹. As power output increased, however, the difference in \dot{V}_{O_2} between the slow and the fast pedalling rates was reduced as the \dot{V}_{O_2} - P relationships converged. In the range from 40 to

100 rev min⁻¹ the convergence was such that there was no significant difference close to, and at $\dot{V}_{O_{2,max}}$. At 120 rev min⁻¹ the \dot{V}_{O_2} was, however, noticeably elevated at all power outputs and although the difference with other pedalling rates was reduced as maximum was approached it was not totally eliminated. The magnitude of this difference is indicated by the fact that while at 50 W power output \dot{V}_{O_2} was 0.43 l min⁻¹ higher at 100 rev min⁻¹ compared to 80 rev min⁻¹, the difference in \dot{V}_{O_2} at 120 rev min⁻¹ compared to 100 rev min⁻¹ was +0.87 l min⁻¹.

Blood lactate

Blood lactate concentration during the incremental tests followed very similar patterns at all pedalling rates except again at 120 rev min⁻¹. Increasing the pedalling rate from 100 to 120 rev min⁻¹ caused a marked upwards shift of the $[La]_b$ -power output relationship (Fig. 2).

$P_{M,max}$

The maximum peak power attained in the sprints ($P_{M,max}$) increased gradually with pedalling rate. The highest values were observed at 100 and 120 rev min⁻¹ while sprinting at 140 rev min⁻¹ resulted in a significantly lower $P_{M,max}$; $P < 0.01$ (mean values were, respectively: 595, 808, 976, 1054, 1049 and 964 W at 40, 60, 80, 100, 120 and 140 rev min⁻¹; Fig. 3).

$P_{I,max}$

The maximum mechanical power attained at $\dot{V}_{O_{2,max}}$ in the incremental tests ($P_{I,max}$) was not significantly different when cycling at pedalling rates between 60 and 100 rev min⁻¹ (362 ± 52 , 372 ± 52 , 365 ± 51 W). However, when cycling at pedalling frequencies of 40 and 120 rev min⁻¹ a significantly reduced $P_{I,max}$ was observed ($P < 0.05$). The $P_{I,max}$ at 40 rev min⁻¹ was 36 W lower than at 60 rev min⁻¹, while $P_{I,max}$ at 120 rev min⁻¹ was 59 W lower than at 100 rev min⁻¹ (Fig. 3).

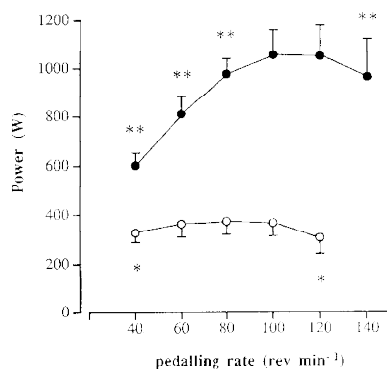


Figure 3

Maximal power output ($P_{I,max}$) reached during incremental tests performed at pedalling rates of 40, 60, 80, 100 and 120 rev min⁻¹ (○) and maximal peak power output ($P_{M,max}$) reached during 10 s sprints performed at pedalling rates of 40, 60, 80, 100, 120 and 140 rev min⁻¹ (●; mean \pm s.d. for 7 subjects). * $P < 0.05$, ** $P < 0.01$, significantly lower than the maximal value.

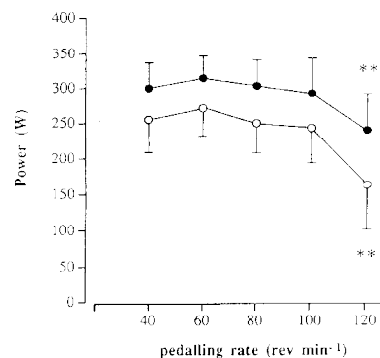


Figure 4

The power output corresponding to 2 ($P_{[La]2}$) (○) and 4 mmol l⁻¹ blood lactate concentration ($P_{[La]4}$) (●) reached during incremental tests performed at pedalling rates of 40, 60, 80, 100 and 120 rev min⁻¹ (mean \pm s.d. for 7 subjects). ** $P < 0.01$, significantly lower than the maximal value.

Power output at lactate threshold $P_{[La]4}$ and $P_{[La]2}$

The $P_{[La]4}$ showed no significant differences when cycling at pedalling rates in the range 40–100 rev min⁻¹ (300 ± 37 , 314 ± 33 , 303 ± 38 , 292 ± 51 W). However, at 120 rev min⁻¹ a significant reduction in $P_{[La]4}$ was observed (240 ± 52 W; $P < 0.01$; Fig. 4). Similarly, $P_{[La]2}$ when cycling in the range 40–100 rev min⁻¹ was not different (255 ± 46 , 271 ± 39 , 250 ± 42 , 243 ± 49 W), but at 120 rev min⁻¹ $P_{[La]2}$ was significantly lower (164 ± 62 W) than at 100 rev min⁻¹ ($P < 0.01$; Fig. 4).

Proportional utilisation of $P_{M,max}$ at $\dot{V}_{O_{2,max}}$ and at the lactate thresholds

In Fig. 3, the power attained at $P_{I,max}$ in each incremental exercise test is shown in relationship to the $P_{M,max}$ – that is the maximal power available at the same pedalling rate. It can be seen that although the power generated at $\dot{V}_{O_{2,max}}$ ($P_{I,max}$) remains relatively constant there is a dramatic increase in the maximum power ($P_{M,max}$) as pedalling rate increases with only a small decrease at 140 rev min⁻¹. As a consequence the proportion of maximum available power utilised to achieve $\dot{V}_{O_{2,max}}$ decreases systematically from 55% at 40 rev min⁻¹ to 29% at 120 rev min⁻¹ (Fig. 5).

The obverse of this is that there is a reserve in the power generation capability of the contributing musculature of 71% at 120 rev min⁻¹ but a reserve of only 45% at 40 rev min⁻¹. Similarly the proportion of the maximum available force utilised at the lactate thresholds also decreases as the pedalling rate increases (Fig. 5). It should be remembered, however, that while there is systematic increase in the percentage reserve of power generating capability at $P_{I,max}$, $P_{[La]4}$ and $P_{[La]2}$ as pedalling rate increases, in absolute terms the $P_{I,max}$, $P_{[La]4}$ and $P_{[La]2}$ are significantly reduced at 120 rev min⁻¹.

DISCUSSION

In these experiments we have examined the external mechanical power delivered by the human locomotory muscles during cycling. We chose to study cycling rather than walking or running because of the relative ease with

which we could measure the forces generated at the foot–pedal interface in this constrained exercise. In addition it was technically rather simple to control pedalling rate with our isokinetic system enabling true maximum force and power to be determined at known movement frequency. In considering the data presented here it should be borne in mind that 120 rev min⁻¹ is in our experience the upper limit of pedalling rate that even trained subjects can maintain for prolonged periods of exercise. It is for this reason that, while we have maximum power data at 140 rev min⁻¹ in order to define the maximum power–movement frequency relationship, we have not attempted to collect data for the incremental experiments at this rate.

In accordance with previous observations (see e.g. Sargeant *et al.* 1981; McCartney *et al.* 1983; Sargeant, 1987; Beelen & Sargeant, 1991) the maximum power output available from the knee extensor muscles showed a parabolic relationship with pedalling rate (see Fig. 3). Thus for any given submaximal mechanical power output the reserve of power generating capability will increase as pedalling rate of the exercise increases, up to approximately 120 rev min⁻¹. On first consideration exercising at pedalling rates which maintain a greater reserve in power generating capability would seem to be advantageous in terms of fatigue resistance (Sargeant & Jones, 1995). Sustained whole body exercise is, however, dependent upon oxygen transport to the working muscle and if there was a difference in the maximum rate at which oxygen could be taken up, transported, and utilised (i.e. $\dot{V}_{O_{2,max}}$) at different pedalling rates this may negate any advantage gained in terms of a greater ‘reserve’ of mechanical power available from the active musculature. Such differences might occur due to the mechanical effect of different pedalling rates on muscle perfusion. The duty cycle, required force, and hence the pattern of intramuscular pressure changes at different pedalling rates could be expected to modify muscle perfusion. At very slow pedalling rates the high forces required per revolution combined with relatively long contractions might reduce muscle blood flow; but equally at very fast pedalling rates, although the forces will be lower

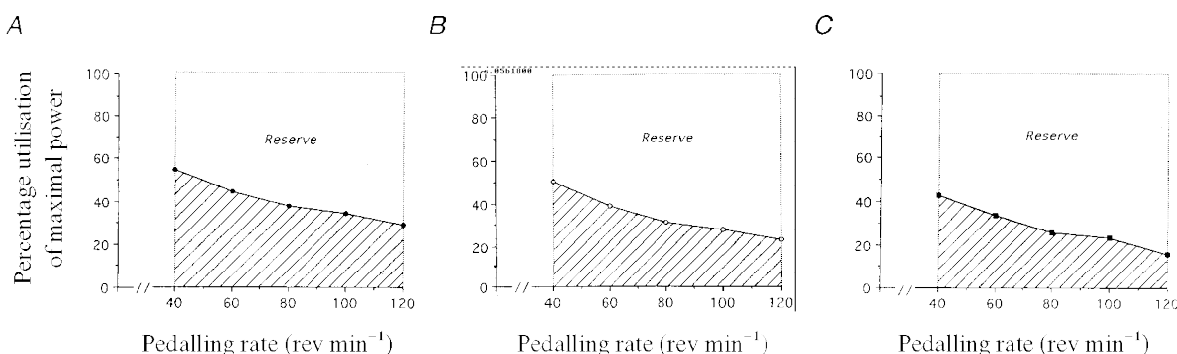


Figure 5

Utilisation of $P_{M,max}$ at $P_{I,max}$ (●, A), at the $P_{[La]4}$ (○, B) and at the $P_{[La]2}$ (■, C), during incremental tests performed at pedalling rates of 40, 60, 80, 100 and 120 rev min⁻¹ (mean for 7 subjects).

per contraction there is relatively less time for reperfusion during the relaxation phase of the duty cycle and this may also compromise muscle perfusion (B. Saltin, personal communication). In fact in the present experiments although the $\dot{V}_{O_{2,max}}$ measured at 40 and 120 rev min⁻¹ (the slowest and fastest pedalling rates) was 5 and 1 % lower than at the intermediate rates this difference was not statistically significant. Thus there is no contra-indication on these grounds to using the fastest pedalling rates during sustained exercise.

If, however, there is no reduction in $\dot{V}_{O_{2,max}}$ at high pedalling rates is it the case that the oxygen cost of delivering useful external power changes? The present data on \dot{V}_{O_2} - P are shown for all subjects in Fig. 1. At the lowest power output of 50 W oxygen cost increases from 40 to 100 rev min⁻¹; however, as $\dot{V}_{O_{2,max}}$ is approached the \dot{V}_{O_2} - P relationships for these pedalling rates converge so that there is no significant difference at $\dot{V}_{O_{2,max}}$ in the useful power delivered. In contrast the oxygen cost of incremental exercise pedalling at 120 rev min⁻¹ is markedly increased compared with the other experiments. For example with an increase of 20 rev min⁻¹ in pedalling rate the \dot{V}_{O_2} required to deliver 50 W of external power increases by 0.43 l min⁻¹ from 80 to 100 rev min⁻¹ but by 2 times that level (0.84 l min⁻¹) from 100 to 120 rev min⁻¹. Furthermore although visual inspection of the data suggest some convergence of the \dot{V}_{O_2} - P relationship at 120 rev min⁻¹ with the other data as $\dot{V}_{O_{2,max}}$ is approached this does not eliminate the difference. As a consequence the external power delivered at $\dot{V}_{O_{2,max}}$ when pedalling at 120 rev min⁻¹ is significantly less by 16 % when compared with pedalling at 100 rev min⁻¹ ($P < 0.05$). Clearly therefore in maximum exercise lasting a few minutes where maximal oxygen transport may play a decisive role the advantage of an increased reserve in power generation at 120 rev min⁻¹ is probably negated by the reduction in the external power that can be delivered for $\dot{V}_{O_{2,max}}$.

There are a number of possible explanations for the marked increased oxygen cost of delivering a given external power when pedalling at 120 rev min⁻¹. One component is certainly the energy cost of mechanical power, which is not measured as useful power performed on the ergometer. This includes the power and associated energy cost required to move the legs themselves (see e.g. Francescato *et al.* 1995) and associated with this it is possible that at high velocities power is less effectively directed at the foot-pedal interface. We did not attempt to measure the energy cost of zero-load pedalling in these experiments since this is in our view difficult and unrepresentative when an ergometer with a free wheel drive is used, as in these experiments. Backward extrapolation of our data in Fig. 1, suggests a mean oxygen uptake of ~ 0.6 l min⁻¹ at 60 rev min⁻¹ for zero load, which is in agreement with previous determinations on a fixed wheel cycloergometer (Davis & Sargeant, 1975), but ~ 3 times that level, that is 1.9 l min⁻¹, at zero load at 120 rev min⁻¹ when the legs are being moved exactly twice as often. When it is remembered that the 0.6 l min⁻¹ at

60 rev min⁻¹ includes the resting O_2 uptake so that moving the legs probably accounts for less than 0.35 l min⁻¹ it will be realised that the increased \dot{V}_{O_2} at 120 rev min⁻¹ represents a ~ 5 times increase in energy cost for moving the legs twice as often!

Although some of that disproportionate increase may be due to the inability to direct the generated leg forces effectively at 120 rev min⁻¹ it is not immediately obvious that there is such a marked change in the pattern of coordination that it could account for a 5 times increase in energy cost.

In the present experiments we also took the opportunity to measure the blood lactate concentration during the incremental test since a number of studies have shown a close association between blood lactate concentrations and exercise tolerance (Kindermann *et al.* 1979; Sjödin & Jacobs, 1981; Tanaka & Matsuura, 1984; Henritze *et al.* 1985; Zoladz *et al.* 1993). In Fig. 2 the individual data are presented. In all subjects the $[La]_b$ - P relationship for all experiments shows a curvilinear relationship. The experiment performed at 120 rev min⁻¹ is, however, consistently displaced to the left of the other experimental data indicating higher blood $[La]$ at every power output. This is partly, but not entirely, due to less power being delivered for \dot{V}_{O_2} at 120 rev min⁻¹. Thus the difference is reduced but not eliminated if $[La]_b$ is expressed relative to percentage $\dot{V}_{O_{2,max}}$. Using the blood lactate concentrations of 4 and 2 mmol l⁻¹ as predictors of exercise tolerance, as proposed by Kindermann *et al.* (1979), Sjödin & Jacobs (1981) and Henritze *et al.* (1985), we have calculated the external power delivered at these concentrations (Fig. 2). Although there is a significant reduction in the external power delivered at these thresholds when pedalling at 120 rev min⁻¹, there is no difference between the experiments at pedalling rates between 40 and 100 rev min⁻¹. These data suggest that compared with other pedalling rates exercise performed at 120 rev min⁻¹ involves greater reliance on anaerobiosis and hence reduced exercise tolerance.

In conclusion the present investigation has examined the effect of choosing different movement frequencies on the physiological demand of sustained locomotion. In so doing it sheds light on optimum strategies for resisting fatigue and hence maintaining power output. The pivotal observation is that due to the parabolic nature of the power-velocity relationship, which indicates an optimal velocity of ~ 120 rev min⁻¹ for maximum power, the delivery of a constant submaximal power output during sustained exercise can be achieved with a increasing reserve of power generating capability as the pedal rate chosen increases up to 120 rev min⁻¹.

At first sight this would suggest an advantage to choosing the fastest pedalling rate of 120 rev min⁻¹ for sustaining high intensity exercise. However, what the present study shows is that although there is no significant difference in the $\dot{V}_{O_{2,max}}$ attained, the external power that can be delivered at $\dot{V}_{O_{2,max}}$ is significantly lower at 40 and 120 rev min⁻¹,

compared with the other pedal rates. This difference in external power delivered at $\dot{V}_{O_{2,max}}$ is also reflected at submaximal exercise intensity, so that the external power output delivered at submaximal exercise intensities, characterised by blood lactate concentrations of 2 and 4 mmol l⁻¹, was also significantly less at 120 rev min⁻¹ compared with exercise performed at 60–100 rev min⁻¹.

Taken together these observations indicate that although it may be generally advantageous to choose faster rather than slower pedalling rates, at 120 rev min⁻¹, the advantage of having a greater reserve of power generation may be negated by the reduction in the external power delivered at earlier onset of anaerobiosis which might be expected to result in earlier fatigue. Finally, it is interesting to note that these results are supported by observations of what competitive cyclists actually do in the 1 h distance event on the track for example. The world holders over the past 50 or more years have consistently chosen a pedal rate of ~105 rev min⁻¹. Equally observations on competitive club cyclists cycling at a speed close to $\dot{V}_{O_{2,max}}$ show that they spontaneously choose a gear ratio that requires about 100 rev min⁻¹ (see Sargeant, 1994).

- BEELLEN, A. & SARGEANT, A. J. (1991). Effect of fatigue on maximal power output at different contraction velocities in humans. *Journal of Applied Physiology* **71**, 2332–2337.
- BEELLEN, A., SARGEANT, A. J. & WIJKHUIZEN, F. (1994). Measurement of directional force and power during human submaximal and maximal isokinetic exercise. *European Journal of Applied Physiology* **68**, 177–181.
- BENEDICT, F. G. & CATHCART, E. P. (1913). Muscular work: a metabolic study with special reference to the efficiency of the human body as a machine. Carnegie Institute Publication no. 187, Washington, DC.
- CARNEVALE, T. J. & GAESSER, G. A. (1991). Effects of pedaling speed on the power-duration relationship for high-intensity exercise. *Medicine and Science in Sports and Exercise* **23**, 242–246.
- DAVIES, C. T. M. & SARGEANT, A. J. (1975). Effects of training on the physiological responses to one and two-leg work. *Journal of Applied Physiology* **38**, 377–381.
- DICKENSON, S. (1928). The dynamics of bicycle pedalling. *Proceedings of the Royal Society B* **103**, 225–233.
- FRANCESCATO, M. P., GIRARDIS, M. & DI PRAMPERO, P. E. (1995). Oxygen cost of internal work during cycling. *European Journal of Applied Physiology* **72**, 51–57.
- HENRITZE, J., WELTMAN, A., SCHURRER, R. L. & BARLOW, K. (1985). Effect of training at and above the lactate threshold on the lactate threshold and maximal oxygen uptake. *European Journal of Applied Physiology* **54**, 84–88.
- HILL, A. V. (1922). The maximal work and mechanical efficiency of human muscles and their most economical speed. *Journal of Physiology* **56**, 19–30.
- KINDERMANN, W., SIMON, G. & KEUL, J. (1979). The significance of the aerobic-anaerobic transition for the determination of work load intensities during endurance training. *European Journal of Applied Physiology* **42**, 25–34.
- KROGH, A. & LINDHARD, J. (1920). The changes in respiration at the transition from work to rest. *Journal of Physiology* **53**, 431–437.
- LUPTON, H. (1923). An analysis of the effects of speed on the mechanical efficiency of human muscular movement. *Journal of Physiology* **57**, 337–349.
- MCCARTNEY, N., HEIGENHAUSER, G. J. F., SARGEANT, A. J. & JONES, N. L. (1983). A constant velocity ergometer for the study of dynamic muscle function. *Journal of Applied Physiology* **55**, 212–217.
- MCCAUGHTON, L. & THOMAS, D. (1996). Effect of different pedalling speeds on the power-duration relationship of high intensity cycle ergometry. *International Journal of Sports Medicine* **17**, 287–292.
- SARGEANT, A. J. (1987). Effect of muscle temperature on leg extension force and short-term power output in humans. *European Journal of Applied Physiology* **56**, 693–698.
- SARGEANT, A. J. (1994). Human power output and muscle fatigue. *International Journal of Sports Medicine* **15**, 116–121.
- SARGEANT, A. J. (1996). Human power output – determinants of maximum performance. In *Human Muscular Function During Dynamic Exercise. Medicine and Sport Science*, vol. 41, ed. MARCONNET, P., SALTIN, B., KOMI, P. & POORTMANS, J., pp. 10–20. Karger, Basel.
- SARGEANT, A. J., HOINVILLE, E. & YOUNG, A. (1981). Maximum leg force and power output of human muscle in maximal cycling exercise. *Journal of Applied Physiology* **51**, 1175–1182.
- SARGEANT, A. J. & JONES, D. A. (1995). The significance of motor unit variability in sustaining mechanical output of muscle. In *Fatigue, Neural and Muscular Mechanisms. Advances in Experimental Medicine and Biology*, vol. 384, ed. GANDEVIA, S., ENOKA, R. M., MCCOMAS, A. J., STUART, D. G. & THOMAS, C. K., pp. 323–338. Plenum, New York.
- SJÖDIN, B. & JACOBS, I. (1981). Onset of blood lactate accumulation and marathon running performance. *International Journal of Sports Medicine* **2**, 23–26.
- TANAKA, K. & MATSUURA, Y. (1984). Marathon performance, anaerobic threshold, and onset of blood lactate accumulation. *Journal of Applied Physiology* **57**, 640–643.
- WILKIE, D. R. (1960). Man as a source of mechanical power. *Ergonomics* **3**, 1–8.
- WILKIE, D. R. (1981). Equations describing power input by humans as a function of duration of exercise. In *Exercise Bioenergetics and Gas Exchange*, ed. CERRETELLI, P. & WHIPP, B. J., pp. 75–80. Elsevier, North Holland Biomedica Press, Amsterdam.
- ZOLADZ, J. A., RADEMAKER, A. C. H. J. & SARGEANT, A. J. (1995). Non-linear relationship between O₂ uptake and power output at high intensities of exercise in humans. *Journal of Physiology* **488**, 211–217.
- ZOLADZ, J. A., SARGEANT, A. J., EMMERICH, J., STOKŁOSA, J. & ZYCHOWSKI, A. (1993). Changes in acid-base status of marathon runners during an incremental field test: Relationship to mean competitive marathon velocity. *European Journal of Applied Physiology* **67**, 71–76.
- ZOLADZ, J. A., SZKUTNIK, Z., MAJERCZAK, J. & DUDA, K. (1998). Detection of the change point in oxygen uptake during an incremental exercise test using recursive residuals: relationship to the plasma lactate accumulation and blood acid base balance. *European Journal of Applied Physiology* **78**, 369–377.

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